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Greater capacity to exploit warming temperatures in northern populations of European beech is partly driven by delayed leaf senescence

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Abstract

One of the most widespread consequences of climate change is the disruption of trees' phenological cycles. The extent to which tree phenology varies with local climate is largely genetically determined, and while a combination of temperature and photoperiodic cues are typically found to trigger bud burst (BB) in spring, it has proven harder to identify the main cues driving leaf senescence (LS) in autumn. We used 905 individual field-observations of BB and LS from six *Fagus sylvatica* populations, covering the range of environmental conditions found across the species distribution, to: (i) estimate the dates of BB and LS of these populations; (ii) assess the main drivers of LS; and (iii) predict the likely variation in growing season length (GSL; defined as the period from BB to LS timing) across populations under current and future climate scenarios. To this end, we first calibrated linear mixed-effects models for LS as a function of temperature, insolation and BB date. Secondly, we calculated GSL for each population as the number of days between BB and LS. We found that: i) there were larger differences among populations in the date of BB than in the date of LS; ii) the temperature through September, October and November was the main determinant of LS, although covariation of temperature with daily insolation and precipitation-related variables suggests that all three variables may affect LS timing; and iii) GSL was predicted to increase in northern populations and to shrink in central and southern populations under climate change. Consequently, the large present-day differences in GSL across the range of beech are likely to decrease under future climates where rising temperatures will alter the relationship between BB and LS. Northern populations are likely to increase their productivity as warmer conditions will enable them to extend their growing season.

Key words (4-6): *Fagus sylvatica*, spring phenology, autumn phenology, environmental factors, provenance effect, climate change

1 Introduction

Plants are changing their phenological cycles in response to current climate change (Chmura et al. 2018). Generally, these changes involve a combination of advances in spring leaf phenology and delays in autumn leaf phenology (Gallinat et al. 2015; Piao et al. 2015; Yang et al. 2017), resulting in a longer growing season (Walther et al. 2002; Estiarte and Peñuelas 2015) and potentially increasing forest net ecosystem productivity (NEP) (Way and Montgomery 2015). Phenological responses to environmental cues are to a large extent genetically determined in trees (Liang 2019). Numerous studies along elevational gradients and experiments in common-gardens have found bud burst (BB) in populations of different origin to occur at different dates in many tree species (Vitasse et al. 2013; Dantec et al. 2015; Sampaio et al. 2016; Kramer et al. 2017; Cooper et al. 2018). Leaf senescence (LS) has been less widely studied in such settings, but it also differs inherently among populations of *Betula pubescens* (Pudas et al. 2008), *Fraxinus americana* (Liang 2015), *Populus balsamifera* (Soolanayakanahally et al. 2013), *Populus deltoides* (Friedman et al. 2011), *Populus tremula* (Michelson et al. 2018; Wang et al. 2018) and *Populus trichocarpa* (Porth et al. 2015). However, it is not yet clear to what extent the genetic determinism and the environmental cues of BB match those for LS, and how the interplay of BB and LS drives among-population variation in growing-season length (GSL) (Signarbieux et al. 2017).

Extensive research has identified cold winter temperatures (i.e., chilling requirements) and accumulated spring temperatures (i.e., forcing requirements) as the main drivers of BB; sometimes coupled with photoperiod (Basler and Körner 2014; Fu et al. 2015) (Fig. 1). The major drivers of LS have been more difficult to identify (Gallinat et al. 2015; Brelsford et al. 2019). A recent meta-analysis showed that summer and autumn temperatures, precipitation and long photoperiod can all

affect LS (Gill et al. 2015). Generally, temperature tends to be predominant at lower latitudes (Pudas et al. 2008; Lang et al. 2019), whereas photoperiod is more important at higher latitudes (Soolanayakanahally et al. 2013; Lang et al. 2019) (Fig. 1). Yet temperature effects on LS are not straightforward: increasing summer and autumn temperatures and even moderate drought can delay LS (Xie et al. 2015), whereas severe drought tends to promote earlier LS (Chen et al. 2015; Estiarte and Peñuelas 2015), (Fig. 1). Finally, high insolation and high photoperiod may also delay LS (Liu et al. 2016a) (Fig. 1). The complex nature of the environmental triggers of LS has to-date hampered attempts to understand the causes of its variation across large geographical scales (Chmura et al. 2018). This uncertainty makes it very difficult to estimate GSL across species ranges. Recent studies based on *in-situ* records and satellite data have shown positive correlations between the timing of BB and LS that tend to stabilize GSL across populations (Keenan and Richardson 2015; Liu et al. 2016b). But this is not a universal finding and the extent to which GSL can change depends on the combination of many factors, as explained in Fig. 1.

		GSL			
Reference	EV	BB_R	LS_R	EV	Reference
(Gárate-Escamilla *et al.*, 2019; Ibáñez *et al.*, 2010; Signarbieux *et al.*, 2017; Yang *et al.*, 2017)	↑ Twin/spr	→ ←	→ ←	↑ Tsum/aut	(Ibáñez *et al.*, 2010; Yang *et al.*, 2017; Fu *et al.*, 2018)
	↓ Twin/spr	→ ←	→ ←	↓ Tsum/aut	
(Basler & Körner, 2012; Gauzere *et al.*, 2017; Malyshev *et al.*, 2018)	↑ Phot	→ ←	→ ←	↑ Phot/In	(Liu *et al.*, 2016a)
	↓ Phot	→ ←	→ ←	↓ Phot/In	(Cooke *et al.*, 2012)
(Basler & Körner, 2014; Vitasse *et al.*, 2017; Malyshev *et al.*, 2018)	↑ Chill	→ ←	→ ←	↑ Psum	(Zu *et al.*, 2018)
	↓ Chill	→ ←	→ ←	↑ Drou	(Wu *et al.*, 2018)

Figure 1. Environmental drivers of growing season length through their effects on bud burst and leaf senescence. GSL: growing season length; EV: environmental variables; BB_R: bud burst response; LS_R: leaf senescence response; Twin/spr: winter and spring temperatures; Tsum/aut: summer and autumn temperatures; Phot: photoperiod; In: insolation; Chill: chilling requirements; Psum: summer precipitation; Drou: drought; Columns EV: up arrow: increase in the environmental variable; down arrow: decrease in the environmental variable; Columns BB_R and LS_R: left arrow: early bud burst/leaf senescence; right arrow: delayed bud burst/leaf senescence; Green colour and green leaf: Reference, EV related to bud burst and BB_R; Orange colour and orange leaf: Reference, EV related to leaf senescence and LS_R. All the combinations of bud burst and leaf senescence responses defining the growing season length are possible.

Fagus sylvatica L. (European beech, henceforth "beech") is one of the most dominant and widespread broadleaf forest trees in Europe (Preston and Hill 1997), and it is of high ecological and economic importance (Packham et al. 2012). In beech, BB responds to a combination of chilling and forcing temperature requirements (Heide 1993; Falusi and Calamassi 2012; Kramer et al. 2017) as well as to photoperiod (Heide 1993; Caffarra and Donnelly 2011; Basler and Körner 2012), with the strength of these drivers changing along environmental gradients. For instance, BB is more affected by photoperiod in colder climates, and by chilling requirements in warmer climates (Gárate-Escamilla et al. 2019). Studies of LS in beech suggest that: (i) temperature may be a more important cue than photoperiod when nutrients and water are not limiting (Fu et al. 2018); (ii) non-senescent green leaves are prematurely lost as a result of severe drought conditions (Bréda et al. 2006); (iv) early BB correlates with early LS (Fu et al. 2014; Chen et al. 2018; Zohner et al. 2018); (v) leaves first start to change colour in autumn from the upper part of the canopy, suggesting that hydraulic conductance or the amount of solar radiation received over the growing

season may play a role in triggering LS (Gressler et al. 2015; Lukasová et al. 2019), although this could also be related to an hormonal effect (Zhang et al. 2011).

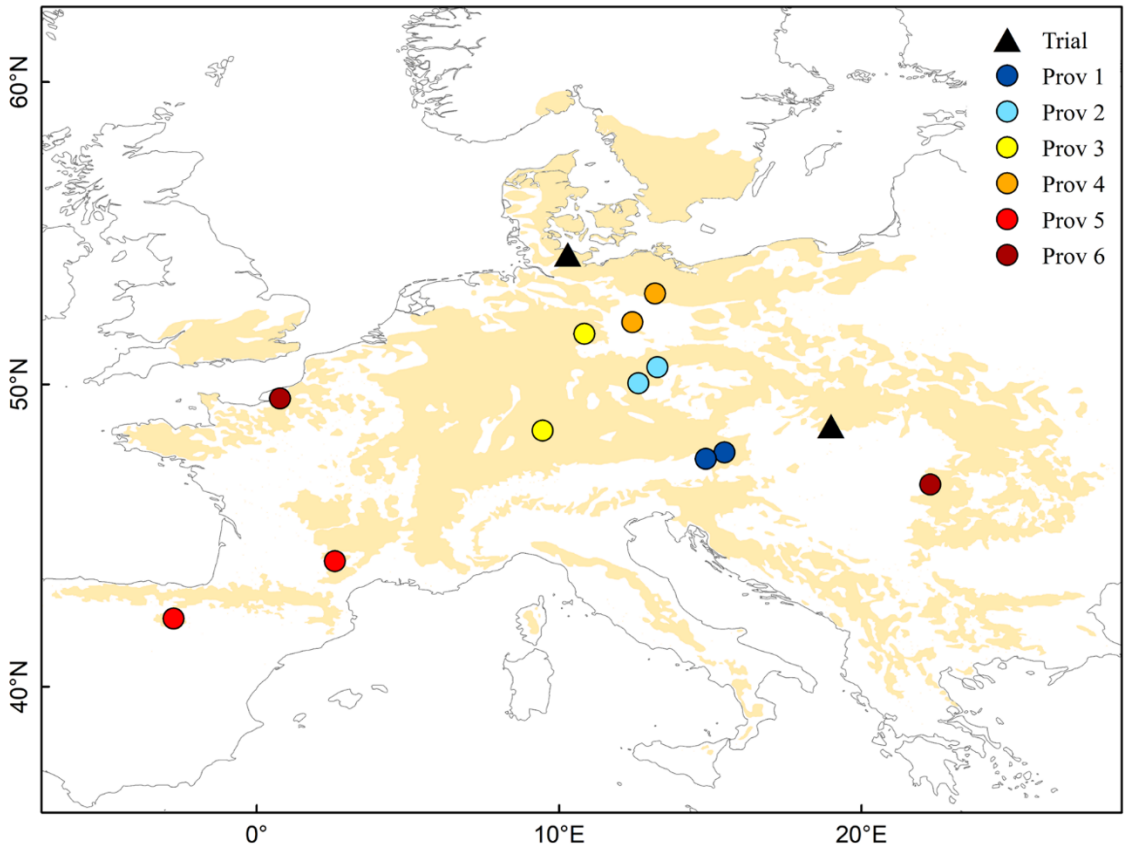
Here, we investigate BB and LS in six different beech provenances (905 trees) planted in two common gardens in central Europe (Robson et al. 2018), and use this information to infer how range-wide patterns of beech GSL might evolve under future climate warming. Specifically, we attempt to: (i) estimate the dates of BB and LS, and how they differ among provenances; (ii) assess the main environmental drivers of LS; and (iii) predict GSL and how it would vary across populations under current and future climate.

2 Materials and Methods

2.1 Field trials and provenances

Spring and autumn leaf phenological observations came from two common-gardens (i.e. provenance tests, genetic trials; hereafter "trials") located in Schädtbek (54.30°N, 10.28°E), Germany, and Tále, Mláčik, Slovakia (48.62°N, 18.98°E) (henceforth termed "Germany" and "Slovakia" trials, respectively). These two tests belong to a large network of beech common-gardens planted to understand the population (i.e. provenance effect including genetics) effects of climate change on fitness-related traits across the distribution range (details given in Robson et al. 2018). These trials were planted with seeds collected from 38 provenances (32 provenances in Slovakia and six provenances in Germany) that roughly span the entire environmental range of beech (Fig. 2, Map). Seeds were germinated in the greenhouse and planted in the trials when two years old, in 1995 (Germany) and 1998 (Slovakia). To maintain a balanced design (same number of provenances per trial), we used only six provenances from each of the two trials (Fig. 2, Map &

Table). The six provenances from the Slovakian trial were chosen based on their similar climatic origin to those planted in the German trial (Pearson correlation $r \geq 0.98$). The provenances were ranked from colder (1) to warmer (6) origins (Fig. 2, Map & Table). Trees growing in Germany were measured at an age of 12 and 13 years, those in Slovakia at 11 and 12 years (Fig. 2, Table).



Provenance Information

T	P	Lon	Lat	Elev	N	NT	Age	BIO 14	Ppet Min	P JJA	Tm JJA	Tm SON	DIM JJA	DIM SON	*r*
G	**1**	15.47	47.75	1171	99	76	12, 13	62.74	39.08	145.31	10.96	2.94	4.77	2.34	0.99
S		14.85	47.53	1223	199	124	11, 12	66.97	45.39	159.62	11.37	3.32	4.77	2.34	
G	**2**	12.62	50.03	909	97	55	12, 13	53.93	-15.57	96.22	13.09	5.00	4.44	1.87	0.99
S		13.25	50.57	795	94	66	11, 12	50.19	-5.59	91.98	13.22	5.23	4.44	1.87	
G	**3**	10.83	51.67	411	109	94	12, 13	55.73	-23.51	86.16	14.72	7.14	4.31	1.77	0.99
S		9.45	48.47	740	180	109	11, 12	50.58	-20.54	105.49	15.42	7.56	5.00	2.21	
G	**4**	13.17	53.00	57	78	58	12, 13	30.00	-58.73	64.89	16.96	8.67	4.29	1.67	0.99
S		12.42	52.05	154	116	81	11, 12	31.85	-69.49	64.42	17.08	8.77	4.36	1.71	
G	**5**	-2.75	42.25	943	80	66	12, 13	42.96	-140.38	47.96	16.83	9.56	5.83	3.02	0.99
S		2.58	44.15	698	79	52	11, 12	52.14	-111.58	65.79	18.05	11.35	5.79	2.88	
G	**6**	22.27	46.68	161	73	57	12, 13	39.27	-104.09	69.63	20.76	11.45	5.14	2.52	0.98
S		0.77	49.53	14	104	67	11, 12	44.52	-86.53	50.84	16.97	11.04	5.04	2.09	

Figure 2. Map: Geographical distribution of beech provenances (coloured circles) and trials (triangles) underlying this study. Beige shading indicates the distribution range of beech. Each circle colour indicates a pair of similar provenances from each trial (the colour gradient depicts the clinal variation from cold [blue] to warm [red] provenances, as defined in Table S1). Table: Climatic and geographic data that were used for merging provenances of similar climatic origin for modeling purposes. As the provenances were not shared between the two sites, we selected provenances of similar climatic characteristics. T: trial where the trees were measured (G=Germany, S=Slovakia); P: number of the provenances as shown in Figure 1; Lon: longitude; Lat: latitude; Elev: elevation (m); N: total number of trait measurements (including repeated measurements over years); NT: total number of individual trees; Age: age of the trees when measured; BIO14: precipitation of driest month; Ppet Min: minimal annual water balance; P JJA: precipitation of January, July and August; Tm JJA: mean temperature of January, July and August; Tm SON: mean temperature of September, October and November; DIM JJA: mean daily insolation of June, July and August; DIM SON: mean daily insolation of September, October and November; *r*: Pearson correlations per pair of provenances accommodated under the same number.

2.2 Estimation of bud burst, leaf senescence and growing season length

We transformed the observational stages (phenophases), and score data (qualitative measurements) for BB and LS to Julian days by fitting the phenophases (Fig. 3 and S1; Table S1 and S2) for each tree in every trial using the Weibull function (Robson et al. 2011; Gárate-Escamilla et al. 2019). The Weibull function is non-linear and asymptotic in the upper and lower limits, hence it requires

154 at least two censuses to obtain a fit of the data: the day of the year (DOY) when BB is attained in
155 spring (stage 2.5; Fig.3 and S1; Robson et al. 2013) and at the stage at which 50% of the trees'
156 leaves have changed colour from green to yellow (stage 3; Fig. 3 and S1; (Lang et al. 2019)). We
157 calculated GSL for each tree as the number of days between the estimated dates of BB and LS
158 (Estiarte and Peñuelas 2015).

159

160 **2.3 Environmental data**

161 To separate the effects of the provenance (genetic effects) from those of the trial (environmental
162 effects), we used the average climate from 1901 to 1990 for each provenance and the average
163 climate during the years of measurement for the trials (Leites et al. 2012) in our models. We used
164 the following precipitation- and temperature-related variables from EuMedClim (Fréjaville and
165 Benito Garzón 2018): precipitation in the driest month (BIO14, mm), precipitation (P, mm) in
166 June, July and August (JJA), minimal (Min) monthly water balance (PPET, mm), and mean
167 temperature (Tm, °C) in June, July and August (JJA) and September, October and November
168 (SON). In addition, we used latitude as a proxy of photoperiod as well as daily insolation, a
169 function of day length and solar irradiance (Yeang 2007). We downloaded daily insolation data
170 from the NASA Atmospheric Science Data Center (https://power.larc.nasa.gov/data-access-
171 viewer/), and we calculated solar radiation (direct and diffuse) over the wavelength range 400-
172 2700 nm incoming on a horizontal surface for a given location. We used insolation including NIR
173 and SWIR, as well as PAR, because the mode of action is still unknown, so a direct heating effect
174 from NIR and SWIR may be important. We calculated the mean daily insolation (DIM, kWh m^{-2}
175 d^{-1}) between the months of June, July and August (JJA) and September, October and November
176 (SON), respectively. As with the climatic variables, we characterized the DIM of the trial as the

177 average between the planting year and the year of measurement. Because the insolation data series
178 from the NASA Atmospheric Science Data Center begins in July 1983, we characterized the DIM
179 of the population as the average between 1984 and 1990 for JJA, and between 1983 and 1990 for
180 SON.

181 We used the 2070 Representative Concentration Pathway (RCP) 8.5 GISS-E2-R
182 (http://www.worldclim.org/cmip5_30s) scenario for GSL predictions under future climate. We
183 deliberately chose only this pessimistic scenario because, for long-lived organisms such as forest
184 trees, it makes little difference whether the projected situation will be reached in 2070 or some
185 decades later.

186

187 **2.4 Statistical analysis**

188 We used a model of BB already calibrated for the same set of trials and provenances (Gárate
189 Escamilla et al. 2019). We then performed a linear mixed-effects model for LS as a function of the
190 combination of environmental variables with BB date as a co-variate. Environmental variables
191 were selected individually to account for separate trial and provenance effects. Our model allowed
192 us to: (i) estimate the date of LS for each of the six pairs of provenances; (ii) compare the date of
193 LS with the date of BB that was already modelled following a similar methodology (Gárate
194 Escamilla et al. 2019); (iii) calculate GSL for each provenance; and (iv) perform spatial predictions
195 of BB, LS and GSL under current and future climate scenarios.

196

197 2.4.1 Environmental variable selection

198 To avoid co-linearity and reduce the number of variables in our models, we only retained
199 moderately correlated variables (-0.5 < r < 0.5) for modelling purposes. The full correlation matrix
200 between all variables is provided in Fig. S2.

201

202 2.4.2 Linear mixed-effects model of leaf senescence

203 We performed a series of linear mixed-effects models of LS as a function of environmental
204 variables from the trial and the provenances, with BB as a co-variable (Equation 1). Each model
205 included one environmental variable from the provenance, one environmental variable from the
206 trial site and BB as fixed effects. The trial, blocks nested within the trial, individual trees and
207 provenances were included as random effects to control for differences among sites and for
208 repeated measurements of the same tree. The general form of the LS model was:

209 $$log(LS_{ijk}) = \alpha_0 + \alpha_1(EP_{ij}) + \alpha_2(ET_{ik}) + \alpha_3(BB_{ik}) + \alpha_4(EP_{ij} \times ET_{ik}) + \alpha_5(EP_{ij} \times BB_{ik})$$

210 $$+ \alpha_6(ET_{ik} \times BB_{ik}) + \beta + \varepsilon$$

211 (Equation 1)

212 Where LS = leaf senescence of the i^{th} individual of the j^{th} provenance in the k^{th} trial; EP =
213 environmental variable that characterizes the provenance site of the i^{th} individual of the j^{th}
214 provenance; ET = environmental variable that characterizes the trial site of the i^{th} individual in the
215 k^{th} trial; BB = bud burst of the i^{th} individual in the k^{th} trial; β = random effects and ε = residuals. In
216 addition, the model included the following interaction terms: EP × ET, EP × BB, and ET × BB.
217 EP × ET. Interactions represent differences in LS values that can be attributed to the interactions
218 between genetic (provenance) and environmental (site) effects. EP × BB and ET × BB interactions

represent the effects of the provenance on LS related to BB and the effects of the site related to BB.

LS models were fitted with the 'lmer' function of the package 'lme4'(Bates et al. 2018), within R statistical framework version 3.2.0 (R Development Core Team 2015). To choose the best supported model, we followed a stepwise procedure: (i) to minimize model complexity and collinearly among environmental variables, we selected the most important variable related to the trial by comparing a series of models that included one environmental variable for the trial and BB, and then selected the best model using the Akaike information criterion (AIC) with criterion delta < 2 (Mazerolle 2006), and the variance explained by the fixed effects (marginal R^2) (Supplementary Table S3); (ii) we chose the optimal random component of the model by comparing the set of models that included different combinations of random effects, the previously selected environmental variable from the trial and BB using restricted maximum likelihood (REML), and selected the best model among them using the AIC criterion; (iii) we retained the best environmental variable related to the provenance comparing the models that included one environmental variable from the provenance, the selected variable from the trial, the BB, the interaction between the three variables and the random terms using maximum likelihood (ML) using the AIC criterion (Supplementary Table S4); (iv) we combined the best optimal random and fixed components (previously selected) and adjusted them using REML to obtain the best performing model.

The goodness of fit of the final models was assessed using two approaches. First, we quantified the percentage variance explained by the model attributed to the fixed effects (marginal R^2) and attributed to the fixed and random effects (conditional R^2). Second, we measured the generalisation capacity of the model using cross-validation with independent data. To this end, we

242 calibrated the model with 66% of the data and performed an independent validation (using Pearson
243 correlations) with the remaining 34% of the data.

244

245 2.4.3 Interactions of leaf senescence with bud burst and environmental variables

246 For the best supported LS model, we analysed the significant interactions (EP × ET, EP × BB, and
247 ET × BB in Equation 1) between LS and the environment (ET; represented by the environmental
248 variable from the trial selected by the best supported LS model) and according to provenances
249 showing early, mean and late BB. We also inspected gradients of GSL for the six provenances by
250 plotting GSL against the environmental variable of the trial selected in the model (ET) and
251 population under current conditions. We predicted the date of LS for the future climate scenario
252 RCP 8.5 using our LS model and the date of BB for the same provenances according to our BB
253 model (Gárate-Escamilla et al. 2019), and plotted the predicted future GSL against ET for each of
254 the provenances.

255

256 2.4.4 Spatial predictions

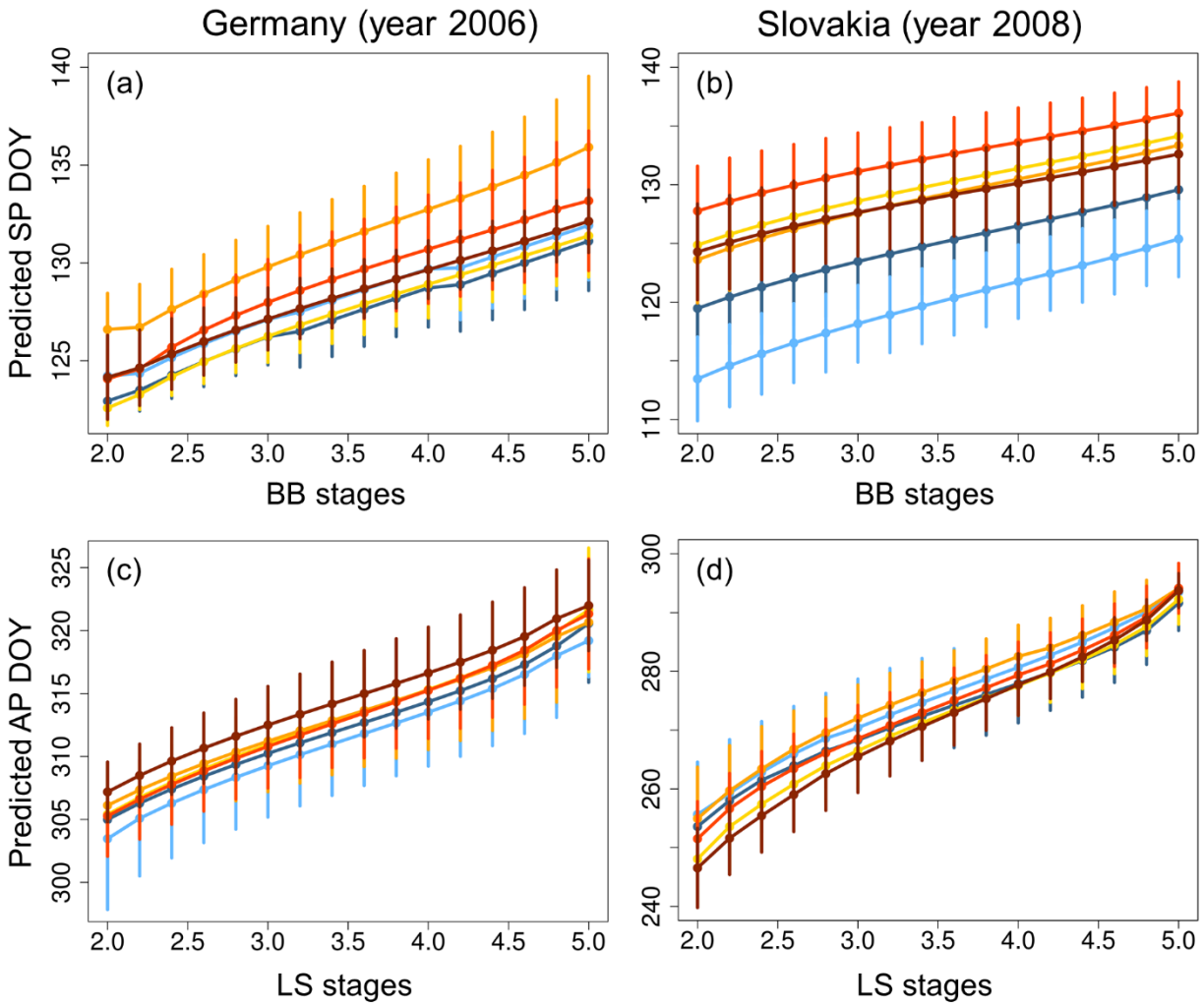
257 Spatial projections of LS were calculated using our LS model for current and future climatic
258 conditions with predictions of BB from Gárate Escamilla et al. (2019). Predictions of GSL were
259 calculated by subtracting the predicted BB from LS for both current and future climatic conditions
260 across the species range. For both current and future predictions, the climate for provenances was
261 represented by the average of the period from 1900 to 1990. The climate of the trials was
262 represented by the average of the period from 2000 to 2014 for current predictions, and by the
263 mean value for the year 2070 according to RCP 8.5 for future predictions.

The current and future spatial predictions of BB and LS include a non-extrapolated area (i.e., predictions including exclusively the climatic range of the two trials, 7.5 to 10°C) and an extrapolated area (i.e., predictions outside the climatic range of the trials) delimited within the distribution range of the species (EUFORGEN 2009). Spatial analyses were performed with the 'raster' package in R (Hijmans et al. 2017).

3 Results

3.1 Estimation of bud burst and autumn leaf senescence dates from field observations

In both trials, differences among provenances were larger for spring leaf flush stages (including bud burst; Fig. 3a & b and S1a & b) than for autumn leaf senescence stages (including 50% yellow leaves; Fig. 3c & d and S1c & d). Although these differences were always statistically significant, they were larger in the Slovakian trial than in the German one (Fig. 3 and S1, Table S1 and S2). Differences in the predicted DOY of spring leaf flush and autumn leaf senescence stages were found for the two years of measurement in both trials (Fig. 3 and S1). We used the fitted data to extract the DOY for the flushing stage 2.5 (bud burst, BB) and the senescence stage 3 (= 50% of leaves yellow, LS) for each provenance (Tables S1 and S2).



Spring leaf flushing phenology stages

2	Buds swollen and elongated.
2.5	Bud burst.
3	First green becomes visible between bud scales, bud adopts a silver-grey sheen.
4	First folded hairy leaves become visible but remain partially held by the bud.
5	Entire leaves cascade from the bud, but are still largely folded and flaccid.

Autumn leaf senescence phenology stages

2	<5% of leaves yellow.
3	<50% of leaves yellow.
4	<100% of leaves yellow.
5	Winter state.

Figure 3. Predicted spring bud burst and autumn leaf senescence phenology, days of the year (DOY) against the observational stages recorded in the field for the two trials. SP: spring bud burst phenology; AP: autumn leaf senescence phenology. Provenance colours range from dark blue

(cold origin) to dark red (warm origin) for the provenances in the two trials (Fig. 2, Map & Table). The spring leaf flushing and autumn leaf senescence stages are described in the lower part of the figure. The phenology stages were recorded in the year 2006 in Germany and 2008 in Slovakia.

3.2 Variable selection and best model selection

Our inspection of climate variables revealed that: (i) provenance and trial variables were not correlated with each other; (ii) temperature (Tm JJA and Tm SON)- and precipitation (BIO14, Ppet Min and Prec JJA)-related variables for the provenances were correlated, whilst daily insolation (DIM JJA and DIM SON) variables for the provenances were only correlated with the latitude (Lat) of the provenances; (iii) all the trial variables were correlated among themselves; and (iv) the co-variable BB was not correlated with the rest of variables (Fig. S2).

In view of these results, we retained daily insolation (DIM JJA and DIM SON) and temperature-(Tm JJA and Tm SON)-related variables for the provenances, all climate variables from the trials, and BB as predictors for our models of LS. The best model according to AIC criteria (Tables S3 and S4) used the mean temperature in September, October and November (Tm SON) of the trial and of the provenance, and BB as a co-variable (Table 1 and Table S3).

Table 1. Statistics from linear mixed-effects models of leaf senescence. Obs: number of trait measurements; Variance: variance explained by the random effects; SD: standard deviation of each level of random effects; Estimate: coefficient of the regression, shown on a logarithmic scale; SE: standard error of each fixed variable; *t*: Wald statistical test that measures the point estimate divided by the estimate of its SE, assuming a Gaussian distribution of observations conditional on fixed and random effects. Fixed effects: coefficients of the fixed effects of the model; BB: bud

burst; Tm SON_T: mean temperature of September, October and November of the trial; Tm SON_P: mean temperature of September, October and November of the provenance. Coefficients of the interactions: BB x Tm SON_T and BB x Tm SON_P. *r*: Pearson correlation; R^2M: percentage of the variance explained by the fixed effects (Marginal variance); R^2C: percentage of the variance explained by the random and fixed effects (Conditional variance).

	Leaf senescence		
Model	Linear Mixed Effect		
	Random Effects		
	Obs	Variance	SD
Population	12	3.33E-05	5.77E-03
Trial	2	2.39E-02	1.55E-01
Trial:Block	6	9.73E-06	3.10E-03
Tree	925	1.88E-04	1.37E-02
Residuals		2.34E-04	1.53E-02
	Fixed Effects		
	Estimate	SE	*t*
Intercept	5.62E+00	1.10E-01	51.16
BB	-8.18E-04	9.91E-05	-8.25
Tm SON_T	2.88E-02	1.43E-02	2.02
Tm SON_P	2.61E-02	8.10E-03	3.23
BB x Tm SON_T	5.97E-04	9.61E-05	6.21
BB x Tm SON_P	-1.96E-04	6.60E-05	-2.97
	r	R^2M	R^2C
	0.92	0.52	0.99

3.3 Leaf senescence model

LS differed among the provenances and between the two trials. These differences were explained by the Tm SON of the trial and provenance, as well as by BB (Table 1). Interactions between BB and Tm SON of the trial and provenance were also significant (Table 1). Late LS timing was related to higher Tm SON of the trial and provenances (Fig. 4). Late LS was related to late BB at high Tm SON of the trial, whilst at low trial Tm SON the opposite effect occurred (Fig. 4a). Late LS was related to early BB irrespective of Tm SON of the population (Fig. 4b). The marginal R^2 was 52%, while the conditional R^2 was 99% (Table 1). The capacity for generalisation from the model was $r = 0.92$ (Table 1).

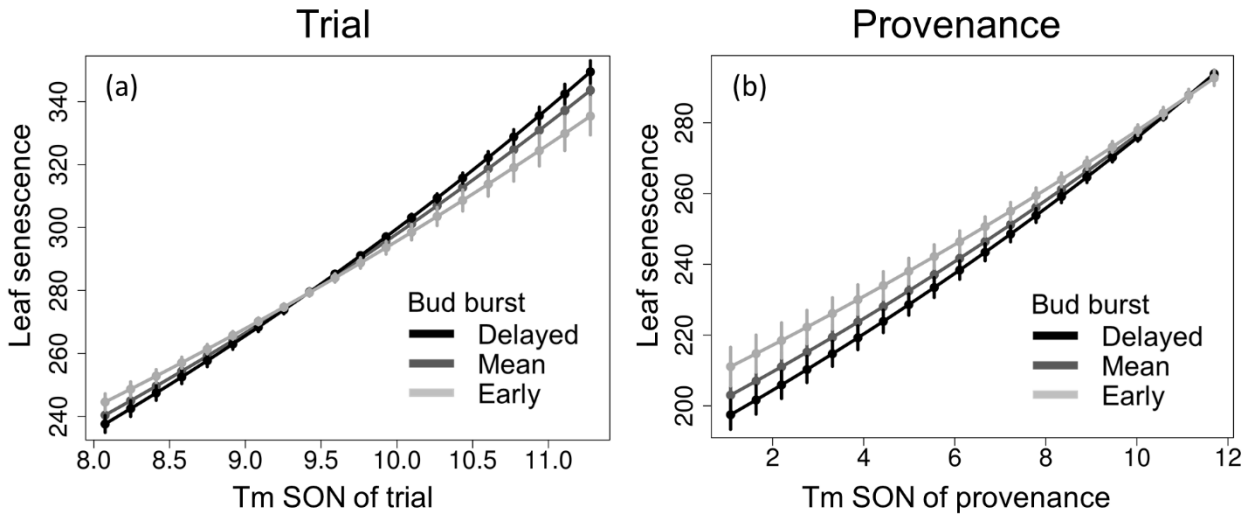


Figure 4. Mathematical interaction between leaf senescence and the mean temperature in September, October and November (Tm SON) for the trial (a) and for the provenance (b). The mathematical interaction is estimated from the LS linear mixed-effects model (equation 1), where BB is considered as a co-variable. Leaf senescence is given in Julian days, and Tm SON in °C. The black line represents delayed bud burst, the dark-grey mean bud-burst and the light-grey early bud-burst. The error bars represent the 95% confidence intervals.

3.4 Determinants of growing season length under current and future climates

GSL greatly increased with higher temperatures in September, October and November in the trials, although the strength of this effect depended on the origin of the provenances (Fig. 5). The increase in GSL was greatest for cold provenances (3.2-5.2 C°), which had their longest GSL under cold conditions (7.5-8.5 C°) at the trials in the current climate (Fig. 5a). In our two trials, GSL differed more among provenances under future than under current autumn temperatures (Fig. 5b). The longest GSL under future conditions was predicted at high trial temperatures (11.5-12 C°) for the warm (10.5-11.3 C°) and cold (3.2-5.2 C°) provenances, whilst at low trial temperatures (10.5-11 C°), the longest GSL was predicted for warmer (10.5-11.3 C°) populations (Fig. 5b).

When we extrapolate our models for the examined 2070 climate scenario, GSL is predicted to increase up to 9 days in the north-east of the range (Fig. 6). Decreases of GSL up to 8 days are predicted for much of the range including the central, southern, western and eastern areas; little or no change in GSL is predicted for the south-eastern-most range (Fig. 6).

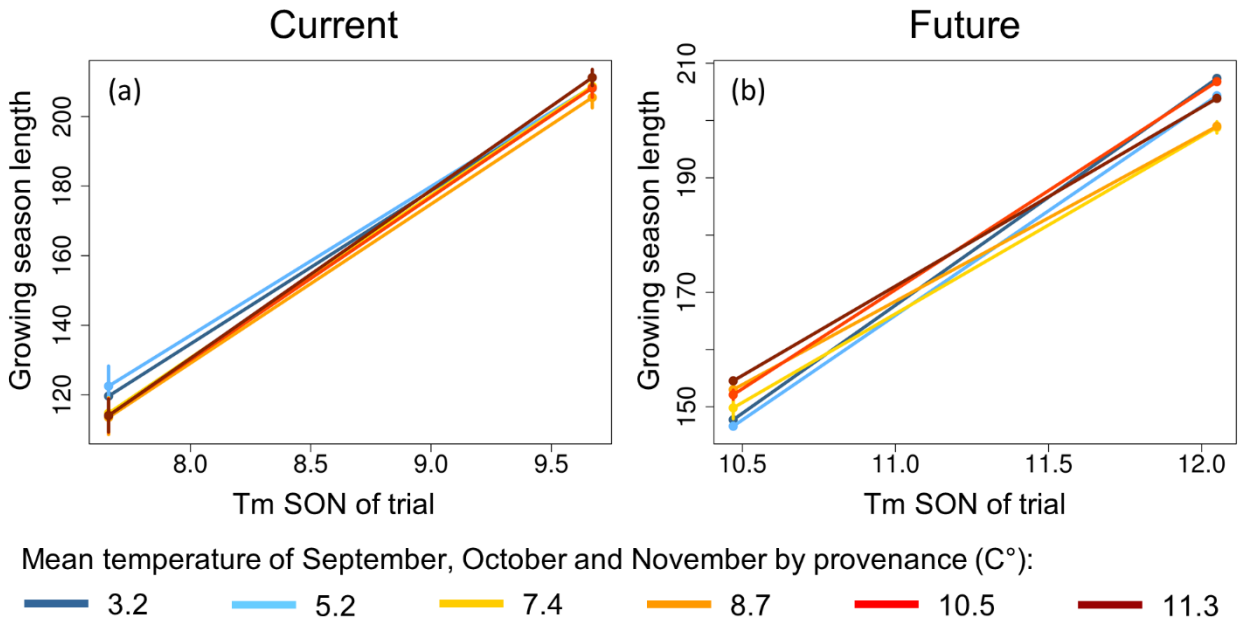
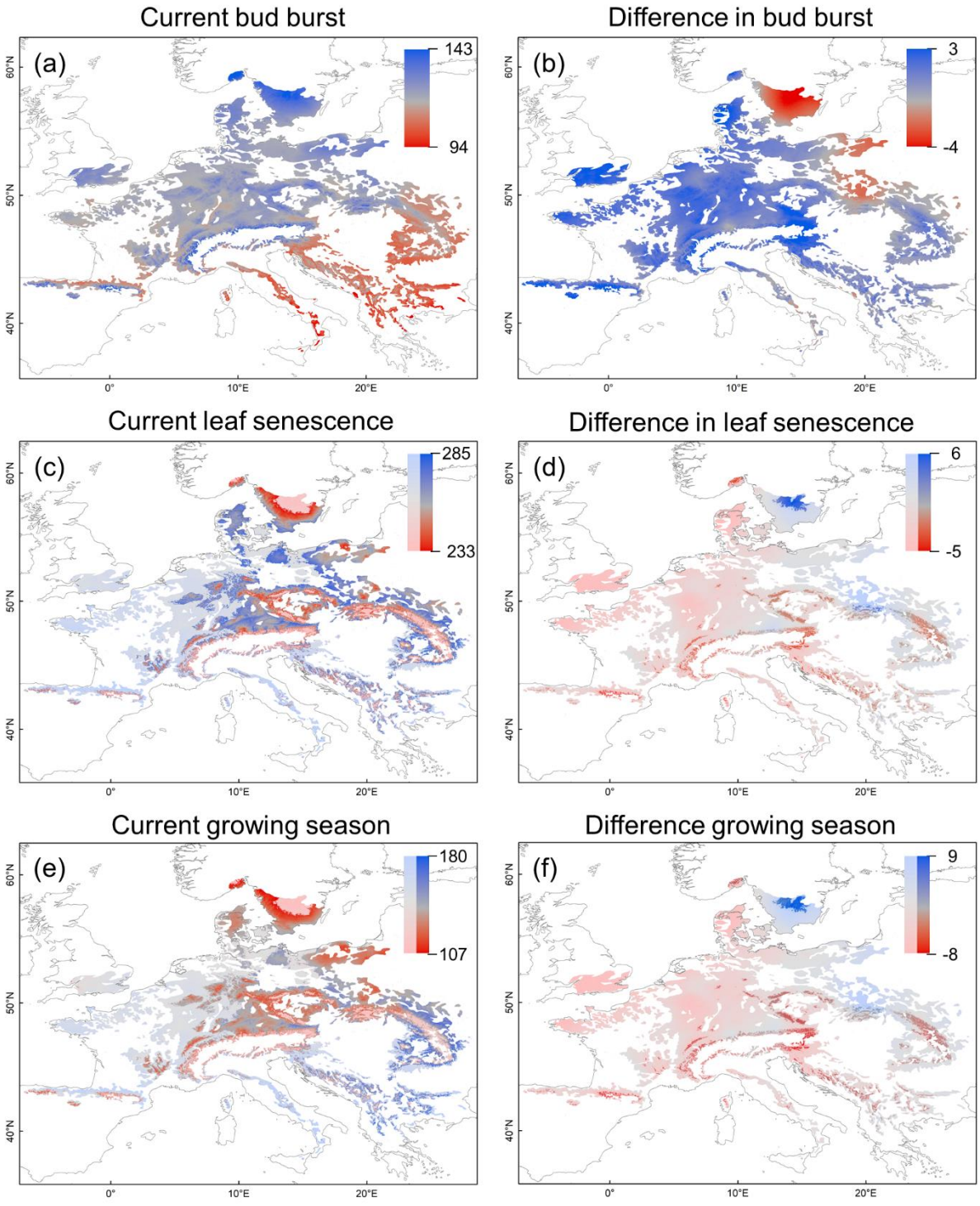


Figure 5. Interaction between growing season length and the mean temperature of September, October and November (Tm SON) of the trial, for (a) current climatic conditions (year of measurement minus year of plantation) and (b) the future climate scenario (RCP 8.5 for 2070). The colour gradient depicts the clinal variation from cold (blue) to warm (red) provenances (Tm SON). Growing season length is represented in days. The error bars represent the 95% confidence intervals.



353

354 **Figure 6.** Spatial projections for (a) bud burst under current climatic conditions, (b) bud-burst

355 differences between current and future conditions, (c) leaf senescence under current climatic

356 conditions, (d) leaf-senescence differences between current and future conditions, (e) growing-

season length under current climatic conditions and (e) growing-season-length differences between current and future conditions. The growing-season length represents the difference between leaf flushing and leaf senescence. The colour gradient depicts the clinal variation from low (red) to high (blue) values of bud burst, leaf senescence and growing-season length. Growing-season length is represented in days, and leaf senescence and bud burst in Julian days. Solid colours represent the predicted geographic area without extrapolation from the climatic area covered by the trials (TmSON = 7.5 to 10°C), the soft colours represent the extrapolated area (that is, outside the range of the calibration) predicted by the models. Current climate refers to the average climate calculated from 2000-2014, and difference in bud burst/leaf senescence/growing season represents the differences between the model predictions for future (2070, RCP 8.5) and contemporary climate conditions for bud burst/leaf senescence/growing season.

4 Discussion

4.1 Provenance differences in bud burst and autumn leaf senescence

The origin of beech provenances is a major determinant of the timing of their leaf spring and autumn phenology (Table 1), which confirms their genetic differentiation in the control of phenology (Chmura and Rozkowski 2002; Petkova et al. 2017, Alberto et al. 2013). This differentiation has often been reported to be stronger for spring phenology than for autumn phenology (Vitasse et al. 2009; Weih 2009; Firmat et al. 2017; Petkova et al. 2017), which is in agreement with what we found in our provenances. For instance, in the Slovakian trial the difference in the date of budburst between colder and warmer provenances was more than 20 days (Fig. 3 and S1). The duration of autumn leaf senescence is longer than that of leaf flushing in beech

(Fig. 3 and S1, Table S1 and S2) (Gömöry and Paule 2011; Petkova et al. 2017), whereas other temperate broadleaf species such as *Salix* spp. and *Quercus petraea* have a relatively long period of leaf-out and relatively abrupt autumn leaf senescence (Weih 2009; Firmat et al. 2017). Although the dates of spring and autumn leaf phenological stages varied between the two years of our study, the same response patterns persisted in both years (Fig. 3 and S1), suggesting a consistent effect of environmental conditions on the trials (Weih 2009; Friedman et al. 2011; Petkova et al. 2017). Our results also revealed larger differences among provenances for both BB and LS in the Slovakian trial than in the German one (Fig. 3 and S1), confirming that, in addition to genetic effects, the environment plays an important role in the phenological response of beech (Vitasse et al. 2013; Gárate-Escamilla et al. 2019).

4.2 Environmental variables defining leaf senescence

Overall, our results support the assertions that (1) high autumn temperatures, both at the site of population origin and at the planting site, delay LS in beech, and (2) early BB tends to be followed by early LS (Table 1). The delayed LS promoted by warmer temperatures that we obtained by manipulating both genetic and site factors using common-garden trials (Fig. 4), is consistent with previous studies based on *in-situ* LS records (Delpierre et al. 2009; Vitasse et al. 2011), satellite data (Yang et al. 2015; Liu et al. 2016a) and climate-controlled chambers (Gunderson et al. 2012; Fu et al. 2018). While the convergence of these studies is reassuring, the extent to which warmer temperatures promote delayed LS still remains elusive (Estiarte and Peñuelas 2015): warmer temperatures accompanied by moderate drought appear to delay LS until a certain threshold (Xie et al. 2015); but beyond this drought threshold LS is accelerated (Chen et al. 2015; Estiarte and Peñuelas 2015). The roles of temperature and drought in LS have several broader implications

because the delay in LS induced by warm temperatures is associated with: delayed degradation of chlorophyll (Fracheboud et al. 2009), maintenance of photosynthetic enzyme activity (Shi et al. 2014), prolonged leaf life span (Liu et al. 2018a), an increased risk of early-autumn frost damage that might kill leaves before nutrient reabsorption is complete (Estiarte and Peñuelas 2015), (Hartman et al. 2013) and a possible increase in photosynthetic carbon assimilation related to a longer growing season (Liu et al. 2016b).

Our findings do not necessarily imply that LS timing in beech only depends on the temperature of the provenance, because this parameter co-varied with daily insolation, latitude and precipitation measured at the origin of the provenance (Fig. S2). These factors explained a low proportion of the overall variance (higher insolation and latitude promoting delayed LS and higher precipitation promoting earlier LS, although delayed LS might be temperature-related due to cold temperatures experienced at high latitudes; see Table S3), yet we cannot exclude the possibility that they may have affected LS timing to some extent. For instance, photoperiod and insolation can have a strong effect on LS at high latitudes (Liu et al. 2016a, b) where photosynthesis at the end of the growing season can be increased by high insolation (which implies high photosynthetically active radiation; Bonan 2002) and by long photoperiods before the autumn equinox. This benefit feeds back, potentially producing a delay in LS as a result of persistent chlorophyll retention under sustained high irradiance (Kim et al. 2008).

4.3 The effect of bud burst on leaf senescence

The significant carry-over effect of BB on LS timing that we found when considering the climate of the trial (Table 1; Fig. 4a) is consistent with other recent studies on beech (Fu et al. 2014; Signarbieux et al. 2017; Chen et al. 2018; Zohner and Renner 2019) and other deciduous trees across the Northern Hemisphere (Keenan and Richardson 2015; Liu et al. 2016b). The relationship between BB and LS is complex and various different mechanisms have been proposed to explain carry-over effects of BB on LS, according to the particular conditions in each study: (i) leaf structural and morphological traits constrain leaf life span (Reich et al. 1992) and programmed cell death (Lam 2004; Lim et al. 2007); (ii) once a plant's carbohydrate storage capacities are saturated, growth is inhibited ("sink limitation") and LS is promoted (Fatichi et al. 2013; Keenan and Richardson 2015; Körner 2015; Signarbieux et al. 2017); (iii) LS is itself affected by the preceding winter/spring temperature (Fu et al. 2014; Signarbieux et al. 2017; Zohner and Renner 2019); (iv) early BB could lead to soil water depletion through increased transpiration, resulting in drought stress and producing earlier LS (Buermann et al. 2013); (v) early BB might increase pest attack (Jepsen et al. 2011) and increase the probability of spring frost damage (Hufkens et al. 2012), leading to an earlier LS. Our use of multiple provenances of different climatic origin enabled us to isolate the genetic component of these carry-over effects of BB on LS from the temperature response. We only found this pattern among cold provenances (3.2-5.2 C°) (Fig. S3) and in regions with high autumn temperature (11.5-12 C°) (Fig. 4a). Yet, we can not rule out the mechanisms listed above, and more experimental testing is needed to further elucidate the relationship between BB and LF across large environmental gradients.

The significant interaction effect of BB and the autumn temperature of the provenances on LS is notable (Table 1), as it suggests that the relationship between BB and LS is moderated by the temperature at the site of provenance origin in a population-specific manner. Contrarily to the

446 carry-over effect that we found between delayed LS and late BB when the autumn temperature of
447 the trial was warm (Fig. 4a), there was an interaction effect between delayed LS and early BB only
448 when the autumn temperatures of the populations were low (Fig. 4b), suggesting that early BB is
449 correlated with delayed senescence only when provenances have cold origins (e.g. from the
450 northern range).

451

452 4.4 Variation in growing season length based on bud burst, leaf senescence and the environment
453 under present and future climates

454 Our results, based on two trials located in the core of the distribution range, predict that almost all
455 the provenancess monitored (except number 3 with an average autumn temperature of 7.4°C)
456 would extend their GSL by up to 10 days under future climatic conditions with increased autumn
457 temperatures (11.5-12 C°) (Fig. 5b). However, caution is required when scaling this result up over
458 large geographical areas with our models based on only two trials. When the models predict
459 phenology for locations within the climatic range of the trials, only trees in northern regions are
460 expected to increase their GSL up-to 9 days. This trend can be attributed to the positive relationship
461 between early BB and delayed LS in cold provenances (Figure 4b), which would extend to north-
462 eastern regions of the species distribution when we extrapolate our results outside the climatic
463 range of the trials (Fig. 6f). The GSL of trees in the rest of the range is predicted by our model to
464 decrease by at least 8 days without extrapolation (Fig. 6). Several recent studies based on field or
465 satellite data have also predict an increase in GSL (Barnard et al. 2018; Liu et al. 2018b; Gaertner
466 et al. 2019) at high latitudes, coincident with cold beech populations. Yet Chen et al. (2018), a
467 study including cold southern beech populations like those considerd here, did not detect increases
468 in the GSL of southern populations of four temperate European tree species (*Quercus robur, F.*

469 *sylvatica*, *Betula pendula* and *Aesculus hippocastanum*) over the last two decades; a study
470 including cold southern populations of beech like those we consider here. These two trends are
471 both consistent with our spatial projection of GSL (Fig. 6). The predicted larger GSL differences
472 in the central and southern range are mostly the result of later leaf senescence predicted for these
473 regions (Fig. 6), which is likely due to an expected increase in autumn temperatures in these
474 regions. We should however note that our spatial modelling results, although covering a wide
475 climatic range, should be interpreted with caution since they are based on empirical data from only
476 two trials, which can limit their scope.

477

478 **5 Conclusions**

479 European beech is characterised by extensive plasticity in many of its life history traits (Gárate-
480 Escamilla et al. 2019) compared to other tree species (Benito Garzón et al. 2019). Yet, strong
481 genetic control over beech phenology, particularly in spring (Kramer et al. 2017), can constrain
482 the acclimative response of populations to climatic changes and hence potentially compromise
483 their future performance. Our analyses provide important insights into the complex relationships
484 driving spring and autumn phenology across the species range. Although our extrapolations are
485 only based on two trials, and hence they do not represent the entire climate conditions that
486 populations encounter across the species range, we found large range-wide differences in GSL (as
487 inferred from BB and LS) under present climate conditions. However, these differences are likely
488 to diminish in the future, because the GSL of southern and core populations (i.e. those with a
489 relatively long current GSL) is predicted to decrease, whilst that of northern and north-eastern
490 populations (i.e. those with a relatively short current GSL) is predicted to increase. These trends
491 are largely driven by an increase in temperatures that would modify phenology. Taken together,

our results suggest that northern populations should increase productivity in the coming years, extending their growing season to take advantage of warmer conditions in the northern part of the range.

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